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Cultural transmission among hunter-gatherers

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We examine from whom children learn in mobile hunter-gatherers, a way of life that characterized much of human history. Recent studies on the modes of transmission in hunter-gatherers are reviewed before presenting an analysis of five modes of transmission described by Cavalli-Sforza and Feldman [L. L. Cavalli-Sforza, M. W. Feldman, Cultural Transmission and Evolution: A Quantitative Approach (1981)] but not previously evaluated in hunter-gatherer research. We also present two modes of group transmission, conformist transmission, and concerted transmission, seldom mentioned in hunter-gatherer social learning research, and propose a unique mode of group transmission called cumulative transmission. The analysis of the additional modes of transmission indicated that cultural evolutionary signatures of vertical transmission, such as the conservation of cultural traits, have been underestimated because previous studies have seldom considered remote generations or distinguished intrafamilial from extrafamilial horizontal and oblique transmission. However, field data also indicate that hunter-gatherer children interacted with and learned from many nongenetically related individuals; about half of children's and adolescents' horizontal and oblique social learning came from nongenetically related individuals. Intimate living conditions of hunter-gatherers provide opportunities for group transmission, and ethnographic evidence presented demonstrates that at least three types of group transmission exist. All three forms of group transmission theoretically contribute to the conservation of culture, homogeneity of intracultural diversity, and high intercultural diversity. Analysis of additional modes of oblique and horizontal transmission and discussion of previous and unique modes of group transmission demonstrate the various mechanisms by which hunter-gatherer children learn and how cultures are conserved and contribute to cumulative culture.

hunter-gatherers | social learning | cultural transmission | child development

Significance

Cultural evolutionary theories have stimulated substantial research on from whom hunter-gatherers learn. Nine modes of cultural transmission are examined among Congo Basin and other hunter-gatherer groups. The various modes help us to understand why several features of hunter-gatherer life, such as egalitarianism and extensive sharing, are highly conserved and similar across diverse natural environments. The modes of cultural transmission demonstrate how cultural skills and knowledge are maintained for long periods of time, providing opportunities for innovation and cumulative culture.

This paper examines what is known about modes of transmission (i.e., from whom children learn) among hunter-gatherers (HGs), with an emphasis on Congo Basin HGs with whom much of the recent research has been conducted. The paper has three parts: 1) a brief review of recent research on the modes of transmission in HGs; 2) an analysis of five modes of transmission described by Cavalli-Sforza and Feldman (1) but not previously evaluated in HG research; and 3) descriptions of three modes of group transmission, including conformist transmission and concerted transmission, seldom mentioned in HG social learning research, and the introduction of an additional mode of group transmission called cumulative transmission.

The paper relies primarily on Cavalli-Sforza and Feldman's (CS&F) theoretical contributions to modes of cultural transmission (CT) because most HG studies of social learning utilize their evolutionary models of vertical (learning from parents), horizontal (learning from members of the same generation) and oblique (learning from nonparental adults) transmission. The models help predict within and between group variability, stability of cultural traits over time, and the evolution of culture. Cavalli-Sforza and Feldman's concepts are recognized internationally and utilized by researchers in multiple disciplines. They also developed the first model and analysis of dual transmission (DT) (2) and Boyd and Richerson's (3) DT theories have made internationally recognized contributions to understanding from whom individuals acquire culture, which they call content biases, and some of these models are evaluated here. However, overall, few HG field studies have systematically evaluated DT models. Likewise, Durham's (4)coevolutionary theories have contributed substantially to understanding cultural evolution but only a few of his concepts are considered here because they have not been utilized in HG field research.

Studying mobile HGs can shed light on how culture is transmitted in contexts with political, gender, and age egalitarianism, extensive sharing beyond the family, and limited exposure to formal education and market integration. While we recognize that there is underappreciated diversity in contemporary and past HGs (5, 6), many scholars consider these features of contemporary HG lifeways to also have characterized the majority of

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human groups throughout our history (7). In HG societies, culture moves between people face-to-face, and spreads between moderately interconnected groups through widespread social networks established and maintained through travel on foot (8–10). These features in particular are likely to have shaped cultural evolution in humans and facilitated adaptation to diverse ecosystems, thus making the study of cultural transmission among contemporary HGs especially valuable. Our analysis focuses on HG childhood and adolescence because this is when most cultural transmission occurs, though we recognize that learning occurs throughout life (11–15). Moreover, Cavalli-Sforza also had an intrinsic interest in HGs and traveled to and organized several genetic and biomedical studies of HGs in the Congo Basin. The first author, a cultural anthropologist, started to collaborate with Cavalli-Sforza in the late 1970s because of their shared interest in Congo Basin HGs.

Pronounced cross-cultural diversity exists in HG lifeways (6), but some elements of their culturally constructed niches are similar across a wide range of natural environments and dramatically impact CT (11, 12). We examine two. First, HG settlement sizes are small and intimate. Camp sizes average about 25 to 35 individuals (13), but can double in size seasonally for social or economic reasons (e.g., funerals, seasonal resources). Intimate living is particularly pronounced in HGs as measured by distances between homes, space available per person in a house, space per person in a bed, frequency of cosleeping at different ages, and frequency of touching during the day (14). For instance, HGs live in homes that average 2.3 m^2 of space per person whereas the average space for individuals in small-scale farming communities and developed countries is 7.0 m^2 and 45.1 m^2, respectively. Comparative studies show HG infants and young children are held significantly longer and breastfed more frequently than are farmer children (14). One of the only studies of adult proxemics in a HG group showed that G/wi males and females were touching or within an arm's reach of someone 48% and 46%, respectively, of daylight hours (15). Among the HG !Kung, Draper states, "As people sit in camp, resting, talking, and doing chores, they prefer to gather in knots or clumps, leaning against each other, their arms brushing, the crossed legs overlapping" (16).

The relatively small camp size is why social learning in HG middle childhood occurs in multiage play groups (17). Camps have 10 to 12 juveniles of mixed ages that spend their days together. Intimate living provides children of all ages with easy access to multiple models with various skills and knowledge levels. Proximity contributes to individuals knowing each other very well, which means transmission can be brief, subtle, nonverbal, and rapid. Intimate living enhances opportunities for group transmission. A child can watch many individuals nearby with the same skill, or many people can respond or comment verbally or nonverbally (by a look or touch) to a nearby child observed practicing a skill or breaching a social norm, such as hitting another child. Learning skills or knowledge from many proximal and trusting people can contribute to the homogeneity of cultural traits and increase the rate of exposure and susceptibility to innovations introduced to the group.

Second, foundational schemas are ways of thinking and feeling that pervade several cultural domains of HG life (11). They include cultural values, attitudes, and perceptions of what is good and beautiful. Durham (4) would call these "secondary value selection" features of culture that influence cultural learning. Three key HG schemas include 1) political, gender, and age egalitarianism, 2) respect for an individual's autonomy, and 3) extensive sharing/giving. An egalitarian ethos contributes to the lack of strong leaders and to relatively equal access to resources between men and women. HGs are constantly reminded that everyone is equal, unlike class-stratified populations where individuals are regularly ranked along multiple dimensions in relation to others, e.g., grades in school, and hierarchy in work settings. Gender egalitarianism and flexibility are demonstrated among Aka net-hunters when some men do not participate because of their engagement in village activities. In these situations, women hunt more than men, organize all female hunting parties, and return rates are better if more than 60% of participants on the hunt are women (18, 19). Respect for an individual's autonomy means one does not tell or coerce others, including children, what to do. Children may decide whether to go hunting or gathering, whom they want to live with if their parents' divorce, or if they want to use knives or cook something over the fire. Finally, a giving or sharing way of thinking permeates HG life and is why they are characterized as highly cooperative (13), have high levels of allomaternal care (20), and regularly share food beyond the household (21).

The foundational schemas impact the modes of transmission and learning in several ways. Egalitarianism means children can acquire knowledge from men or women as well as young and old members of the community. Children are seldom intimidated by the gender, age, status, skills, or knowledge of others in the group. Respect for autonomy amplifies self-motivated child learning, encouraging children to explore the natural environment and material artifacts. Respect for autonomy also increases adult's tolerance of children wanting to learn and minimizes teaching interventions by others. The desire by others, regardless of gender or status, to help children learn is part of the giving ethos, but the help is restrained in part due to the value placed on respecting the child's autonomy (22, 23).

These features of the HG culturally constructed niche facilitate rapid and easy CT that occurs early in life. A cross-cultural study of 23 HG groups found that 45% of a broad range of skills and knowledge such as how to use knives to prepare food, how to hold, soothe, and wash a baby, how to cook, share food with everyone in camp, and identify, extract, and prepare edible plants, were transmitted by age six or seven (24). A study of Aka HG learning (25) found that 10-y-old children knew 70% of the essential skills and knowledge necessary to survive in the forest. Complete competence for many skills and knowledge occurs by early adolescence (26, 27), but peak efficiency for other skills such as medium and large game hunting or nut cracking does not occur until middle adulthood (12, 13).

Recent Research on Modes of CT in Hunter-Gatherers

Cultural anthropologists have been interested in how children acquire cultural beliefs and practices for almost 100 y (28), but they have yet to systematically focus on from whom children learn at different ages. Cavalli-Sforza and Feldman (1) provided a theoretical framework and stimulation to conduct more extensive systematic studies of the roles of parents, peers, siblings, and nonparental adults in CT.

The initial field study with HG to evaluate CS&F models was conducted with the Aka of the Central African Republic. Adults, children, and adolescents were asked about how they learned 50 skills and knowledge; the study found that vertical transmission was the dominant mode of transmission across most domains. Other early retrospective interview studies with the James Bay Cree (29) and Efe (30) HGs also found that parents were primary transmitters. Early cross-cultural surveys (31, 32) also emphasized the roles of parents.

A cross-cultural analysis of 23 HG groups in the electronic Human Relations Area Files (24) and a recent retrospective interview study with the Tsimane' HG of Bolivia (27) found significant contributions by parents to child learning in several domains. However, these more recent studies were different from the earlier studies in that they showed that, on average, nonparental adults made substantial contributions to child learning, from 25% in the Tsimane' study to 35% in the cross-cultural study. The Tsimane' research (26) was also significant because it found that individuals learned about emerging market economies from same generation family members (horizontal transmission) and that grandparents transmitted oral traditions and vanishing skills seldom used today, both of which were consistent with CS&F predictions (see below for more on grandparents). Both early or recent retrospective interviews or cross-cultural studies indicate that parents are more important than any other family category, e.g., grandparents, aunts/uncles, or siblings, and that horizontal transmission is limited in HG.

A recent shift from interviews to observational studies of social learning has provided more detail about how age and context impact from whom HG children learn. Observational studies with infants and young children up to about four indicate that parents are often near their children and contribute significantly to transmission (32). An observational study of infant teaching, defined as modifying one's behavior to help another learn, among the Aka found that parents provided 71.4% of all teaching episodes (33), and a cross-cultural study of 23 HG groups found that parents transmitted 59.0% of all skills and knowledge during infancy and early childhood (24).

Parents may be important transmitters early in life, but detailed observational studies of middle childhood found that same generation youth were the most frequent contributors to learning (22, 34, 35). Observational research with Martu of Australia and Hadza of Tanzania also revealed that children went foraging without adults and learned from older children and adolescents (36, 37). Anthropologists have recognized for a long time (38, 39) that HG children spend much of their day in multiaged play groups at these ages, in part due to the relatively small size of HG camps, but what early ethnographers did not recognize is that children are actively teaching other children (22, 35). Observational studies also show that this is an essential time for children to practice and experiment with skills (40), often through play with other children (41, 42).

Recent field and cross-cultural studies have also highlighted the importance of nonparental transmission and have provided details on the age and contexts of oblique transmission. Oblique transmission occurs regularly in adolescence, possibly to acquire complex skills, such as spear hunting, religious beliefs, healing practices, and how to make a canoe or basket (43–46). For instance, Dira (43) asked 28 Ethiopian Chabu HG male adolescents how they learned to spear hunt; 60% said they learned from nonparental adults, and only 14% mentioned their fathers. Lew-Levy (47) asked 23 BaYaka male adolescents a similar question about how they learned to spear hunt; 78% said they learned from nonparental adults, and 19% listed their father. Jordan (46) describes Siberian and other northern HG nonparental adults' contributions to how adolescents and young adults learn complex technologies such as canoes, skis, and plank houses.

Overall, recent HG data suggest three culturally constructed niches of development that influence from whom children learn. The first occurs from birth to about 4 y old when infants and young children are often breastfeeding, child mobility is limited, and parental investment in holding, maintaining proximity, and providing is high. This niche enables young children's easy and low-cost learning and contributes to high levels of vertical transmission. Shennan and Steel (31) hypothesized that vertical transmission should be intensive during this early phase of life and then decline to free up parents for future children.

Children's environment is shaped by the second niche at around 5 y old when they transition from regular proximity to parents to spending time in multiage play groups. Until about 12 y old, this niche consists of settings for horizontal transmission, practice, and trial-and-error experiments with skills and knowledge. At around 13 y old until marriage, children move gradually into a third niche, where they spend considerable time with same-sex, similar age peers (e.g., traveling, sleeping together) and start to spend more time with nonparental adults as they learn more complex skills and knowledge, contribute to subsistence, and search for mates. These three culturally constructed developmental niches are common to HG in diverse ecological settings and are consistent with the multistage learning model of Reyes Garcia et al. (42)

The multistage model (48) applies to many small-scale cultures. The HG developmental niches are relatively distinct from those in non-HG because 1) they occur within the context of the two general cultural niches described above (foundational schema and intimate living) which are less frequent in non-HG groups, and 2) social-demographic settings vary. HG wean later and parents are more likely to cosleep than non-HG impacting the first developmental niche, group size is smaller in HGs which impacts the second niche, and the geographic distances of social-mating networks is greater in HG which impacts the third niche (26).

The three development niches are also broad generalizations and do not capture the pronounced diversity and flexibility observed in HG children's learning environments. For instance, among the Efe of the Democratic Republic of Congo, infertility and early weaning are more common than in other HG so children move into the multiage group earlier than in other groups and nonparental adults are more likely to be around for teaching and learning because many adults have no or few children. Variability also exists within groups as HG generally have concentration-dispersal settlement patterns which means that at least part of the year they live in larger groups where access to same-sex and age mates would be greater along with other learning opportunities (49).

Recent research has shown that different methods to measure HG cultural transmission have strengths and weaknesses and may lead to different results. For instance, retrospective interviews with 50 Chabu adult men about how they learned to spear hunt found that 80% mentioned their father (vertical), whereas when 28 Chabu adolescent males were asked prospective questions about with whom they prefer to go spear hunting, 42% mentioned nonparental adults (oblique) and only 14% mentioned father. Adolescents wanted to learn to hunt with trusted/loved older friends, good teachers, or someone with good hunting skills (43). Parents are likely to be important in retrospective interviews with adults because the questions encompass the lifetime of the adult, parents introduce most skills and knowledge in infancy and early childhood, parents cosleep with children to about age 10 and may transmit knowledge at night, parents subtly invest at all ages because of inclusive fitness and social-emotional attachment, and adult's responses may reflect cultural models of who is expected to transmit traits.

The use of cross-cultural databases, such as eHRAF, is helpful for a basic understanding of both universality and diversity in HG cultures. However, the ethnographies used in the HG samples are limited because the researchers seldom conducted child-focused studies and, therefore, made generalizations of transmission based on a limited number of informal observations. Prospective interviews are helpful because they identify with whom children are currently learning and can provide insights into how children

Table 1. Percentage of skills and knowledge acquired by different modes of transmission as reported by 421 Tsimane' adults (81 skills for males and 62 skills for females)

	Vertical	Remote generation	Intrafamilial horizontal	Extrafamilial horizontal	Intrafamilial oblique	Extrafamilial oblique
Male participants	45.5	8.7	14.9	6.1	15.7	2.6
Female participants	53.3	9.5	15.3	4.2	12.8	1.7

Table constructed from figure 1 in ref. 26.

build upon previous skills or knowledge, but we do not know from whom they learned earlier. Focal follow observational studies are an excellent way to obtain details about from whom children learn, the contexts of learning, and cross-check interview data. However, time limitations (usually 4 to 8 h per child) mean these provide a limited snapshot of daily life.

Over the past 40 y, CS&F's theoretical models of CT have generated multiple studies from whom HG learn. The initial field study and some of the most recent research have shown that vertical is an important mode of CT. However, observational and prospective interview studies have demonstrated that children teach other children and that nonparental adults are frequent transmitters of culture in adolescence. The studies have contributed substantially to our understanding of how a child's age, gender, skill complexity, and trust in or skill of the transmitter can influence from whom a child learns.

Expanded Categories of Vertical, Horizontal, and Oblique Transmission

This section examines five modes of transmission described by CS&F (1) but not modeled mathematically and never (as far as we know) evaluated in field studies. We reanalyze our field interview and observational data to understand their frequency and contexts. The five additional modes of transmission include the following (1; 55–56):

Intrafamilial Oblique—closely related adult family members other than parents in the parental generation.

Extrafamilial Oblique—distantly related adult members of the social group in the parental generation.

Remote Generations—grandparents, great-grandparents, or strong oral traditions left by elders.

Intrafamilial Horizontal—siblings and other closely related family members in the same generation.

Extrafamilial Horizontal—contact with unrelated individuals of the same generation (includes peers).

The expanded modes provide greater precision about generational differences, i.e., grandparents have a separate category (some researchers have included them in oblique), and the genetic relationships between transmitter and learner, i.e., intrafamilial and extrafamilial horizontal and oblique forms of transmission. CS&F (1) indicate that intrafamilial horizontal and oblique transmission interact with vertical transmission, which means that they may amplify some of the evolutionary properties associated with vertical, e.g., maintaining the status quo when environmental conditions are stable and contributing to intracultural diversity. Likewise, with remote generations, they state, "…a society in which 'elders' are important in addition to parents, will be more conservative, i.e., show less evolution and a smaller within group variation than a society in which elders are less influential…grandparents or previous generations may not be alive to influence cultural transmission (44: 48, 44)."

The expanded categories indicate that additional forms of cultural transmission may lead to the conservation of culture and other cultural evolutionary properties generally associated with vertical transmission. They may also clarify which modes contribute to culture change and the spread of innovations. Quantitative models indicate that culture change and the spread of innovations can be rapid with horizontal and oblique transmission if contact between individuals is frequent (1), especially in changing and stochastic environments where parental skills may be outdated (3). Intrafamilial contact may be frequent, but the skills and knowledge transmitted may be similar to those of parents. Hypothetically, extrafamilial horizontal and oblique transmission may be the sources of innovation and rapid acceptance of innovations.

We used the additional modes of transmission to reanalyze interview and observational CT data. Results are summarized in Tables 1–4 (see *SI Appendix*, sections 1 and 2 for ethnographic background of the Tsimane' and the Congo Basin ethnic groups (Aka, Baka, BaYaka) as well as actual numbers for percentages in the tables). Genetic relatedness of 0.125 or greater was used as the measure of intrafamilial. The reference in each table provides the original source and research methods for the study. Table 1 is constructed from Fig. 1 in the retrospective study by Schniter et al. (26) and shows that Tsimane' adult males acquired 84.8% and adult females acquired 90.0% of cultural skills from within the family (sum of vertical, remote, intrafamilial horizontal and oblique), percentages that are not that different from the 84.5% of transmission from parents and grandparents in the first retrospective interview study of HG CT (25). The contributions of grandparents were higher in this study than in the others because informants were asked how they learned oral traditions and vanishing aspects of Tsimane' culture.

Table 2 examines with whom Baka children participated during subsistence activities and shows that children spent 81.5% of their time with same-generation children and that they spent more subsistence time with both extrafamilial children (horizontal) and adults (oblique) than they did with intrafamilial children or adults. The table demonstrates the significance of other children (horizontal) in CT. The demographic setting of this Baka group impacts the results. The Baka are active HG but spend much of the year in sedentary villages, and the village in this study was large, with about 250 inhabitants. Hunter-gatherer children go where they want during the day, and these children had many more opportunities to spend time with children of similar age and gender than those in the other studies in the table. Children did not spend much time foraging with grandparents.

Table 3 is a more precise measure of CT because the studies used systematic observational techniques to measure from whom and how children and adolescents learned skills and knowledge. Both studies show that 1) vertical transmission is substantially lower than in Table 1 and other retrospective interview studies with adults, 2) grandparental transmission is limited, especially in adolescence, and 3) extrafamilial transmission is higher, sometimes substantially, than intrafamilial transmission in both ethnic and age groups.

BaYaka extrafamilial horizontal transmission is higher than among the Aka, and extrafamilial oblique transmission is higher in the Aka than in the BaYaka. The variability may be due to differences in what the researchers coded during their

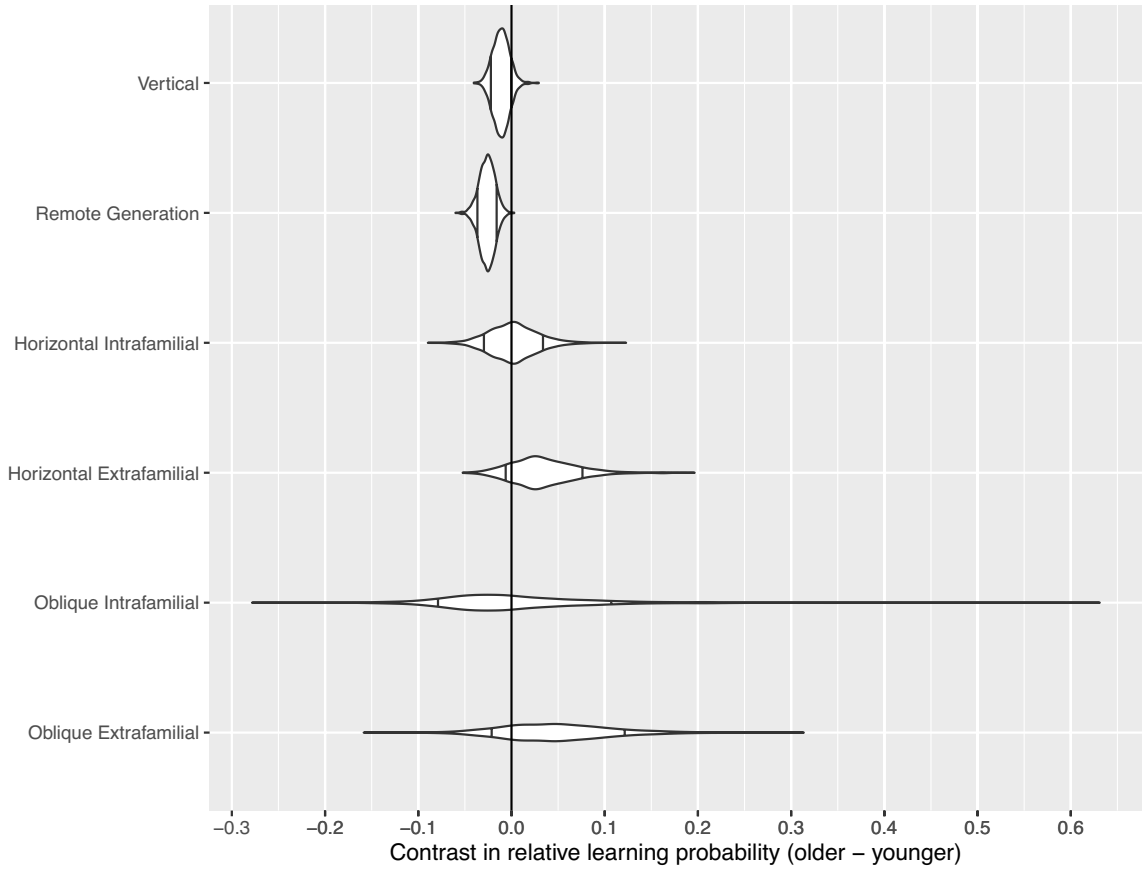


Fig. 1. Contrasts between older and younger Aka children in relative probability of learning via each mode. This figure shows the difference in the distribution of Bayesian posterior probability density estimates of Aka children of ages in the middle-childhood and adolescent developmental niches, given the relative frequency of encounters with these social partners. Estimated contrasts below zero indicate more learning by younger children via that mode, and estimated contrasts above zero indicate more learning by older children via that mode. The degree to which the probability density estimates exclude zero indicates the relatively greater likelihood that there is a true difference between older and younger children in the probability of learning via that mode (equivalent to a "significant" difference in frequentist statistics). The distance from zero of the probability density estimates reflects the relative effect size of the contrast between younger and older children. The interior lines within the density estimates show the 0.11 and 0.89 quantiles (50).

observations; the BaYaka study coded from whom children acquired subsistence skills, while the Aka study coded for learning all forms of skills and knowledge. Religious beliefs and social norms are more opaque and unobservable than subsistence skills, and their complexities may contribute to higher levels of extrafamilial transmission in adolescence rather than middle childhood. Children know fundamental religious beliefs and social norms early in life, but the complexities and depth of knowledge come in adolescence from older adults outside of the family (44).

Table 4 examines the expanded modes of transmission with interviews with BaYaka adolescents about how they learned (retrospective) and how they want to learn (prospective) one skill, spear hunting. The table shows relatively equal contributions to CT by male genetic and nongenetically related individuals (44.4% genetically related with retrospective and 50.8% with prospective), 2) infrequent contributions by grandfathers, 3) no contributions by males of the same generation, and 4) relatively few differences in responses to retrospective and prospective questions.

Another strength of observational data is that it can be used to model the likelihood of social learning from specific individuals given their relative frequency in proximity to learners. A multilevel Bayesian social relations model was built using vertical and the five expanded CT modes to address this. The model was designed to estimate the relative likelihood of the focal child learning via each mode across childhood and adolescence given their relative availability as a social partner (see *SI Appendix* for details). Fig. 1 presents the results for the Aka and indicates that given their relative presence as a focal child's social partners, vertical and remote generation modes are greater in younger children and quickly decrease as a source of cultural learning; horizontal modes of transmission remain relatively steady throughout childhood and adolescence; and both oblique modes, especially extrafamilial, tend to increase as children enter adolescence.

Table 2. Percentage of dyads with whom 58 Baka children 5 to 16 y old of Cameroon reported that they engaged in subsistence activities with (hunting, gathering, fishing, and household maintenance) during the day

	Vertical	Remote generation	Intrafamilial horizontal	Extrafamilial horizontal	Intrafamilial oblique	Extrafamilial oblique
Male informants	4.7	0.5	36.0	51.9	1.6	5.3
Female informants	3.9	0.5	36.7	42.5	1.3	15.0

Reanalysis of data from ref. 34.

Table 3. Percentage of modes of transmission for all forms of social learning (observation and teaching) from observations of 50 Aka children and adolescents of the Central African Republic and all forms of teaching from observations of 36 BaYaka children and adolescents of the Republic of Congo

	Vertical	Remote generation	Intrafamilial horizontal	Extrafamilial horizontal	Intrafamilial oblique	Extrafamilial oblique
Aka middle childhood	14.1	2.3	27.9	28.4	5.9	21.4
Aka adolescence	14.4	0.0	4.9	22.8	19.8	38.1
BaYaka middle childhood	10.7	1.1	20.6	53.6	1.9	12.1
BaYaka adolescence	4.8	0.0	18.4	67.6	3.9	5.31

Reanalysis of Aka data from ref. 22 and BaYaka data from ref. 35.

Like studies reviewed in the previous section, methods matter. Several factors contribute to variability in results: behavioral observations of actual transmission versus interviewing individuals about how they learned skills, the use of retrospective versus prospective questions about learning, the cultural skills and knowledge included in interviews about transmission, the ages of children observed, the items coded in behavioral observations, and the size of camps. Despite this variability, several general patterns emerged from these reanalyses: 1) If one considers vertical, remote generations, and intrafamilial horizontal and oblique transmission, contributions from genetically related individuals are substantial. Genetically related investment is highest, in the 70 to 80% range, in retrospective interviews with adults about a lifetime of learning and about half that amount (27 to 49% in Table 3) in observational methods of child learning; 2) Grandparents infrequently transmit culture, especially in observational studies of middle-aged children and adolescents; 3) Extrafamilial horizontal and oblique transmission are greater than intrafamilial horizontal and oblique transmission (Tables 2–4), especially later in childhood, once controlling for opportunities for interaction (Fig. 1); 4) Minor gender differences exist in from whom HG learn (Tables 1 and 2).

The reanalysis of HG cultural transmission data using the expanded number of modes of transmission has several implications for CT theory and understanding from whom HG children learn. First, the cultural evolutionary signatures of vertical transmission are probably underestimated in HGs because previous studies have yet to consider remote generations and intrafamilial horizontal and oblique transmission. Second, on the other hand, data on the additional modes of transmission indicate that HG children interact with and learn from many nongenetically related individuals. Observational and interview studies (Tables 2–4) show that about half of children's and adolescents' horizontal and oblique social learning comes from nongenetically related individuals, i.e., CT is not biased toward genetically related siblings or aunts/uncles. Third, grandparents and parents may not show up frequently in childhood observational studies of CT, but, at least in early childhood, their investment is high relative to the amount of time they are in proximity to children during the day. Fourth, extrafamilial horizontal and oblique modes may be better candidates for the spread of innovations than are intrafamilial horizontal and oblique modes. Future studies may clarify the similarities and differences in the evolutionary properties of these types of transmission.

Modes of Group Transmission

As described, HGs live in small, intimate settings conducive to easy and rapid group transmission. Few systematic HG field studies exist on group transmission, but long-term child-focused studies provide rich ethnographic examples of various forms of group transmission. Here, we briefly examine two mathematically modeled forms of group transmission, conformist bias, and concerted transmission, introduce an additional type not considered in previous studies, which we call "cumulative transmission," and provide ethnographic examples of each.

The six modes of transmission described in the previous section are not restricted to dyadic interactions. Field data (interviews, observations) are collected and analyzed in ways that give this impression, but this was not the intent of the CS&F models. This section examines three modes of group transmission and all of them could include any mixture of the six models described above.

Cultural evolutionary theorists have modeled several ways in which skills and knowledge of the group can impact the distribution of these cultural traits among individuals, including group effect (51), conformist bias (2, 46), and concerted or many-to-one transmission (52). Group effect models were the first to recognize that the cultural beliefs and practices of members of an entire group can impact the individual. The modeling found that "The main effect of the group …is the stabilization of its variation within the group, which offers fairly fast and establishes quickly a 'mode' [mean] of the trait" (51). Group effect does not explain how individuals acquire the cultural traits from the group.

Another mode of transmission described by Cavalli-Sforza et al. (52) is many-to-one or concerted transmission. This mode occurs

Table 4. Percentages of modes of transmission that BaYaka of the Republic of Congo (N = 20) adolescents mentioned when asked retrospective (Who previously taught you to spear hunt?) and prospective (Who would like to learn to spear hunt from?) questions about spear hunting

	Vertical (fathers)	Remote generation	Intrafamilial horizontal	Extrafamilial horizontal	Intrafamilial oblique	Extrafamilial oblique
BaYaka retrospective	18.5	3.7	0.0	0.0	22.2	55.6
BaYaka prospective	15.9	0.0	0.0	0.0	34.9	49.2

Reanalysis of BaYaka data from ref. 47.

when a group with "many transmitters, potentially even the whole group, apply the same cultural pressure on individuals in the next generations" (52). Original descriptions of concerted transmission focused on efforts by the older generation to transmit knowledge to younger generations, such as with adolescent initiation ceremonies. However, recent research shows that individuals of all ages can transmit cultural values in concerted ways (45). Concerted transmission can be oblique (e.g., initiation) or a mixture of horizontal and oblique. The arrows in Fig. 2 show that the concerted transmission can come from both juveniles and adults and that transmission often occurs through various forms of teaching.

Concerted transmission is central to maintaining HG's foundational schema of egalitarianism and sharing. For instance, if a BaYaka male is aggressive, boastful, or does something inappropriate or dangerous, he is mimicked and the target of laughter and ridicule by groups of BaYaka women (53). Individuals can be reminded that they are no better than others through rough joking and laughter by the group about the looks, smell, size, or shape of their genitals (54). Public mocking and humiliation are used to sanction Hadza children who do not share (55). Concerted transmission in HGs can be synchronous, such as when everyone in the group makes sounds of disgust when a child does not share food or hits another child, or it can take place over days or months during adolescent initiation ceremonies. More systematic research is needed on this regularly used transmission mode in HGs.

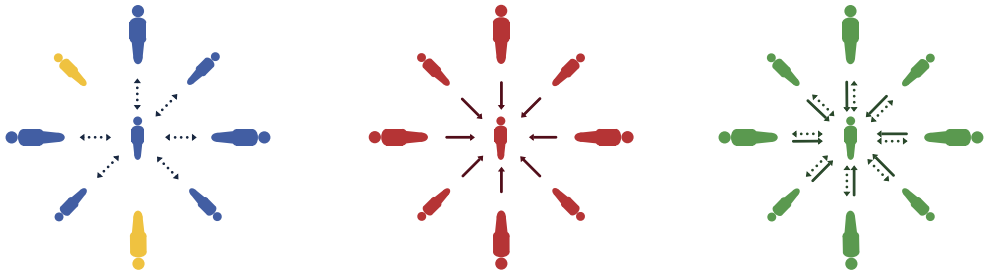
Durham's (4) imposition transmission, where external or internal subgroups use coercive force to transmit culture, is one type of concerted transmission. Imposition appears to be rare in traditional mobile HG groups because of foundational schema, but today could be a useful concept for understanding the impact of external agencies on HG cultures, such as forced sedentarization by national governments or removal of HGs from parks and reserves by international conservation agencies.

Boyd and Richerson (3) identify another form of frequency-dependent group transmission, called conformist bias, where individuals adopt the most frequently observed traits. A variation of frequency-dependent bias associated with conformist bias is nonconformist bias, where an individual does what everyone else is infrequently or not doing. What the group is doing may be perceived as something other than adaptive so that individuals may do the opposite. It is group transmission because it assumes the individual has observed the trait in the group but decides to do the opposite. Fig. 2 shows that the individuals learn via observation and imitation and that the child can learn from both juveniles and adults.

Learning to dance and sing among the Aka are examples of conformist and nonconformist bias. Forty-one percent of Aka adults said they learned specific dances or songs by watching and listening to many others (25). However, group dances and songs also have structures whereby everyone in the dance group can improvise and create complex movements or sounds on the observed patterns (49). The jazz-like innovations are examples of nonconformist bias. Children and adolescents look around and learn the most common patterns, and then they use the knowledge from the group to innovate.

Conformist and concerted transmission are different, almost the opposite of each other, in that conformist transmission involves individuals deciding which skills to copy based on their frequency in the group, whereas, in concerted transmission, members of the group decide what is essential for an individual to learn (Fig. 2). On the other hand, several of their evolutionary properties are similar. Both increase intracultural homogeneity and intercultural diversity of traits, contribute to the conservation of traits, and decrease rates of cultural change. Both can facilitate group selection and be adaptive in stable environments, and both can lead to maladaptation.

Finally, the third mode of group transmission we are calling cumulative transmission. This mode of group transmission refers to specific knowledge or skills that individuals acquire from repeated multimodal experiences and interactions with several group members with those skills or knowledge. The dashed arrows



Evolutionary Properties	Conformist Bias	Concerted Transmission	Cumulative Transmission
Intracultural variation	Low	Low	Low
Intercultural variation	High	High	High
Control of transmission	Individual	Group	Varies
Culture change	Intermediate, can be rapid	Conservative	Conservative
Acceptance of innovation	Can be easy	Difficult	Difficult
Maladaptation	Possible	Possible	Less likely
Examples	Dress, dance	Social norms, religion	Cooking, language, gender roles

Fig. 2. Three modes of group transmission. The two-way arrows in conformist transmission refer to an adaptive strategy where the juvenile looks at all adults (large images) and juveniles (smaller images) in the group and copies the most common trait (individuals in blue). The solid arrows in concerted transmission refer to adults and juveniles teaching cultural skills or knowledge that they feel are important to transmit to the juvenile. Compliance of individuals is expected. The two-way arrows in cumulative transmission refer to the self-motivated juvenile watching, listening, and interacting with many adults with a trait and modifying the trait with more encounters. The solid arrows refer to direct teaching of traits by adults and juveniles. The teaching may be spontaneous or concerted.

in both directions in Fig. 2 represent the self-motived strategy of the child to learn by observation and interactions with others, while the solid arrows show that others can use diverse teaching methods to transmit the skill or knowledge to the child. It is cumulative because the transmission builds upon the child's previous lived experiences with that skill or knowledge, i.e., it involves scaffolding of abilities. For instance, the Aka are net hunters, and children watch adults use and make nets; they pick up nets sitting around camp and try to trap chickens; parents give them a small nets to practice, they participate in net-hunts with adults and other children, others provide advice on how to net-hunt, they hear about problems and watch others mimic and joke about people who made errors on the hunt (chasing game away from instead into nets), and listen to imaginative colorful stories about net hunting around the campfire in the evening. Learning to net hunt is multimodal, interactive, and cumulative.

Learning to share is also acquired by cumulative transmission. When young Aka children take pieces of food from other children or take more than their share out of the family pot, everyone around them makes noises to curb the inappropriate behavior (concerted). Children also learn to share by watching women divide game animals and then being asked by the women to take the different game segments to particular other people. After the food has been prepared, children are asked by their parents to take plates of the food to every other household in the camp. Since huts are only a few meters away, children watch and hear how other children receive negative reinforcement when they do not share or hear comments when someone comes into camp and is ridiculed for eating honey before returning and sharing with others. When children play together, they take insects or a mouse that they capture and divide it equally among all the other children around them. Finally, children hear dramatic stories at night of what happens to people or animals that do not share.

Cumulative transmission uses a template similar to attachment theory (56). If infants receive daily repetitive prompt and sensitive care, they develop "internal working models" of trust to anticipate what to expect from others in the future. Children who receive inconsistent care from others develop ways of thinking and feeling that distrust others. Trust is acquired through the cumulative transmission of children's regular multimodal lived interactions within the group. The cumulative transmission of sensitive care in early childhood is more common among HG than it is with children in other modes of production and is hypothesized to be linked to trust and extensive giving beyond the household in HG, i.e., trust that others will give in the future (57).

Cumulative transmission is how cultural knowledge or skills become "embodied" in a child. Daily physical movements and social-emotional-cognitive actions and interactions shape the child's neuromuscular, endocrine, nervous, and other bodily systems. The skills and knowledge become part of an individual's embodied capital (58). Repeated actions and interactions contribute to establishing cultural habits or customs, such as where and how to urinate and defecate, using utensils or hands to eat, and brushing or washing one's teeth. Embodied cultural traits are highly conserved unless substantial changes occur in the social–ecological setting.

This mode of group transmission builds upon Quinn's ideas (59) about how children learn cultural schema, Bourdieu's concepts of *habitus* and cultural reproduction (60), and Rogoff's (61) concept of intent participation because all of them emphasize the significance of repeated daily experiences within the group for acquiring cultural skills and knowledge. Unfortunately, these theoretical contributors provide limited guidance on research methods to measure cumulative transmission.

Cumulative transmission is like conformist and concerted transmission in that it emphasizes the impact of the group, can contribute to the conservation of cultural traits, is adaptive in stable environments, and can include both horizontal and oblique transmission. Cumulative transmission may include the other two types of group transmission, such as when the child looks around to see whether the skills they want to learn are common (conformist) or when the child regularly receives negative feedback from many members of the group when they slap/hit another child (concerted). Conformist and concerted transmission can also have cumulative features, e.g., children making observations over time to determine the most frequent traits (conformist) or adolescent initiation rituals that take years to complete (concerted). Cumulative is different from the other two forms of group transmission in that it is more interactive/transactional, multimodal (conformist focuses on visual observations; concerted utilizes verbal and other forms of teaching), and child-motivated; assumes regular, frequent interaction with the group, and takes place over long periods, i.e., cultural learning from others is not a one-shot experience; it occurs over extended periods in culturally constructed developmental niches.

Intimate living in HGs enhances the opportunities for group transmission, and ethnographic evidence demonstrates that several types of group transmission exist in HGs. All three forms of group transmission presented theoretically contribute to the conservation of culture, homogeneity of intracultural diversity, and high intercultural diversity. Conformist transmission has been hypothesized to contribute to group selection and extensive cooperation in humans (3), but the other two modes presented also have similar evolutionary features. While group transmission occurs regularly in HG life, Bombjaková's research (53) is one of the few to focus on this form of CT, especially compared to the multiple HG studies of vertical, horizontal, and oblique transmission. More systematic research and better field methods are needed to capture the nature and forms of HG group transmission.

Discussion

Several of the additional modes of transmission and the three modes of group transmission contribute to stabilizing and conserving culture in HGs. The additional modes of remote generation and intrafamilial horizontal and oblique amplify the vertical properties of CT. The models may help to explain the wide range of HG cultural traits that are remarkably similar across a broad range of natural environments, including the three foundational schema and intimate living described in the introduction, an immediate return lifestyle (62), patterns of infant and early child care (extensive holding, breastfeeding, responsive care, and allomaternal care) (63), the three developmental niches of cultural learning, dome-shaped houses, multilocal postmarital residence, and bilateral inheritance (64). Cross-cultural studies show that HGs in Africa share more cultural similarities than African farming and pastoralist cultures (61). A study of 172 native North American cultures, many of which are HGs, found that conservative cultural transmission as measured by culture history was the primary determinant of a broad range of human behaviors, including technology, marriage and family organization, kinship systems, and settlement pattern, rather than the ecological environment (65). Certainly, pronounced cross-cultural diversity exists in gender egalitarianism and other features of HG life (6). However, the various modes of transmission and their associated predictions from mathematical models help us understand some commonalities across diverse landscapes.

The Modes of Transmission Also Contribute to Our Understanding of Cumulative Culture and Cooperative Breeding. Most studies of cumulative culture focus on the processes of how children learn, such as teaching (66), rather than the modes of transmission. While language, teaching, and overimitation may be relatively unique human cognitive abilities that enhance "high fidelity" (low error) transmission, the modes of transmission can contribute to cumulative culture theory in two ways. First, the conservative features of several modes of transmission contribute to maintaining cultural traits in the group for a long time. The stability of traits over time is an essential feature of cumulative culture, as a cultural trait needs to stay in the population long enough for individuals to modify the existing trait (67). Second, some modes of transmission, such as concerted and cumulative transmission, may contribute to high fidelity by repeatedly correcting and advising children about subsistence skills or social norms.

Several modes of transmission contribute to the conservation of culture, but HGs are also known for being flexible and innovative (68). At least four features of HG life and cultural niche construction contribute to regular innovations. The foundational schema of respecting an individual's autonomy means children can explore, do what they like, practice skills independently without interventions from parents and other adults, and innovate. Second, as mentioned in the description of learning to dance and sing, HGs often have social structures that encourage creativity and nonconformity. Hunter-gatherers value creativity in certain domains so much that they incorporate it into their social organization. Third, HGs, especially children, have plenty of leisure time—even in groups like the Hadza, where children regularly contribute to subsistence—and research has shown that leisure time contributes to child learning and creativity (69). Finally, intimate living may not be the source of innovations but can enhance exposure, susceptibility, and the rapid spread of innovations.

The modes of transmission also contribute to understanding the nature of cooperative breeding. Most studies of cooperative breeding in humans emphasize how people other than mothers, especially grandmothers (70), provide direct care and provisioning to infants and young children (20). Theoretical models and characteristics of cooperative breeding often come from studies with nonhuman cooperative breeders. However, humans are distinct from nonhuman animals in that individuals and groups transmit thousands of cultural traits to children necessary to become successful adults. Few cooperative breeding studies have considered the complex nature of investment in CT in humans (71). The multiple forms of CT demonstrate that many people from diverse groups (peers, siblings, distant relatives) invest heavily for years to transmit culture. Research also questions the significance of grandparents in CT.

Conclusion

Intimate living and foundational schema are characteristic features of hunter-gatherer life that impact from whom children learn. Three culturally constructed developmental niches were described and how they impact from whom children learn at different ages.

The analysis of the additional modes of transmission indicated that cultural evolutionary signatures of vertical transmission, such as the conservation of cultural traits, have been underestimated because previous studies have seldom considered remote generations or distinguished intrafamilial from extrafamilial horizontal and oblique transmission. However, field data also indicated that HG children interacted with and learned from many nongenetically related individuals; about half of children's and adolescents' horizontal and oblique social learning came from nongenetically related individuals. Cultural transmission was not biased toward genetically related siblings or aunts/uncles. Grandparents and parents did not show up frequently in observational studies of learning in middle childhood and adolescence, but may be relatively more important in early childhood, despite their overall relatively infrequent proximity. The intimate living conditions of hunter-gatherers provide opportunities for group transmission, and ethnographic evidence demonstrates that at least three types of group transmission exist. Theoretically, all three forms of group transmission contribute to the conservation of culture, homogeneity of intracultural diversity, and high intercultural diversity. The recent research, analysis of additional modes of transmission, and the discussion of previous and unique modes of group transmission demonstrate the various mechanisms by which hunter-gatherer children learn, culture is conserved, and contribute to cumulative culture.

In the last 50 y, extensive research with HGs has been guided and stimulated by CT and DT theories. The cultural evolutionary approaches have contributed substantially to a better understanding of HG social learning, microevolutionary processes, the daily lives of children, and the nature of HG cultures. While we have come a long way since the initial studies with HGs, more field research is desperately needed on all forms of group transmission, especially conformist and cumulative transmission, because they occur regularly in HGs and are essential for understanding the transmission, persistence, and changes in the foundational schema that are at the core of HG life. Current CT research is limited because most of the research has been conducted with Congo Basin HG and existing interview and focal behavioral observation methods are structured for measuring dyadic transmission. Studies with HG from other parts of the world and innovative field methods are needed in future studies to capture the complexities and subtleties of group transmission.

Data, Materials, and Software Availability. All study data are included in the article and/or *SI Appendix*. Data on the Aka, BaYaka, and Baka can be accessed in previous publications cited in the tables in the text. Specific data on each ethnic group are also available upon request from the ethnographer; A.H.B for the Aka, S.L-L for the BaYaka and S.G. for the Baka. Data and codes for Fig. 1 are available on GitHub: https://github.com/ahboyette (50).

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1. L. L. Cavalli-Sforza, M. W. Feldman, *Cultural Transmission and Evolution: A Quantitative Approach* (Princeton University Press, 1981).
2. M. W. Feldman, L. L. Cavalli-Sforza, Cultural and biological evolutionary processes: Selection for a trait under complex transmission. *Theor. Popul. Biol.* **9**, 239–259 (1976).
3. R. Boyd, P. J. Richerson, *Culture and the Evolutionary Process* (The University of Chicago Press, 1985).
4. W. H. Durham, *Coevolution: Genes, Culture and Human Diversity* (Stanford University Press, 1991).
5. M. Singh, L. Glowacki, Human social organization during the Late Pleistocene: Beyond the nomadic-egalitarian model. *Evol. Hum. Behav.* **43**, 418–431 (2022).
6. R. L. Kelly, *The Lifeways of Hunter-Gatherers: The Foraging Spectrum* (Cambridge University Press, ed. 2, 2013).
7. F. W. Marlowe, Hunter-gatherers and human evolution. *Evol. Anthropol.* **14**, 54–67 (2005).
8. R. Whallon, Social networks and information: Non-"utilitarian" mobility among hunter-gatherers. *J. Anthropol. Archaeol.* **25**, 259–270 (2006).
9. A. B. Migliano *et al.*, Characterization of hunter-gatherer networks and implications for cumulative culture. *Nat. Hum. Behav.* **1**, 0043 (2017).
10. K. R. Hill, B. M. Wood, J. Baggio, A. M. Hurtado, R. T. Boyd, Hunter-gatherer inter-band interaction rates: Implications for cumulative culture. *PLoS One* **9**, e102806 (2014).
11. B. L. Hewlett, "Innovation, processes of social learning, and modes of cultural transmission among the Chabu adolescent forager-farmers of Ethiopia" in *Social Learning and Innovation in Contemporary Hunter-Gatherers*, H. Terashima, B. S. Hewlett, Eds. (*Replacement of Neanderthals by Modern Humans Series*, Springer Japan, 2016), pp. 203–215.
12. A. H. Boyette, "Playing with knives: Children's learning contexts and the cultural evolution of technical flexibility" in *The Evolution of Techniques: Rigidity and Flexibility in Use, Transmission, and Innovation*, M. Charbonneau, Ed. (MIT Press, 2024), pp. 121–138.
13. R. B. Lee, R. Daly, "Foragers and others" in *Cambridge Encyclopedia of Hunters and Gatherers*, R. B. Lee, R. Daly, Eds. (Cambridge University Press, 1999), pp. 1–7.
14. B. S. Hewlett, J. Hudson, A. H. Boyette, H. N. Fouts, "Intimate living: Sharing space among Aka and other hunter-gatherers" in *Towards a Broader View of Hunter-Gatherer Sharing*, D. Friesem, N. Lavi, Eds. (McDonald Institute Conversations, McDonald Institute for Archaeological Research, 2019), pp. 39–56.
15. K. Sugawara, Spatial proximity and bodily contact among the Central Kalahari San. *Afr. Study Monogr.* **3**, 1–43 (1984).
16. P. Draper, Crowding among hunter-gatherers: The !Kung Bushmen *Science* **182**, 301–303 (1973).
17. M. Konner, *The Evolution of Childhood: Relationships, Emotion, Mind* (Harvard University Press, 2010).
18. A. J. Noss, B. S. Hewlett, The contexts of female hunting in Central Africa. *Am. Anthropol.* **103**, 1024–1040 (2001).
19. J. Hoffman, K. Farquharson, V. V. Venkataraman, The ecological and social context of women's hunting in small-scale societies. *Hunter Gatherer Res.* **7**, 1–32 (2023), 10.3828/hgr.2023.8.
20. S. B. Hrdy, *Mothers and Others: The Evolutionary Origins of Mutual Understanding* (Belknap Press of Harvard University Press, 2009).
21. M. Gurven, To give and to give not: The behavioral ecology of human food transfers. *Behav. Brain Sci.* **27**, 543–583 (2004).
22. A. H. Boyette, B. S. Hewlett, Autonomy, equality, and teaching among Aka foragers and Ngandu farmers of the Congo Basin. *Hum. Nat.* **28**, 289–322 (2017).
23. A. H. Boyette, S. Lew-Levy, Socialization, autonomy, and cooperation: Insights from task assignment among the egalitarian BaYaka. *Ethos* **49**, e12284 (2021), 10.1111/etho.12284.
24. Z. Garfield, M. Garfield, B. S. Hewlett, "A cross-cultural analysis of hunter-gatherer social learning" in *Social Learning and Innovation in Contemporary Hunter-Gatherers: Evolutionary and Ethnographic Perspectives*, H. Terashima, B. S. Hewlett, Eds. (Springer Japan, 2016), pp. 19–34.
25. B. S. Hewlett, L. L. Cavalli-Sforza, Cultural transmission among Aka Pygmies. *Am. Anthropol.* **88**, 922–934 (1986).
26. E. Schniter, H. S. Kaplan, M. Gurven, Cultural transmission vectors of essential knowledge and skills among Tsimane forager-farmers. *Evol. Hum. Behav.* **44**, 530–540 (2023), 10.1016/j.evolhumbehav.2022.08.002.
27. S. Lew-Levy, R. Reckin, N. Lavi, J. Cristóbal-Azkarate, K. Ellis-Davies, How do hunter-gatherer children learn subsistence skills?: A meta-ethnographic review. *Hum. Nat.* **28**, 367–394 (2017).
28. M. Mead, *Coming of Age in Samoa: A Psychological Study of Primitive Youth for Western Civilization* (Morrow Quill Paperbacks, 1928).
29. K. Ohmagari, F. Berkes, Transmission of indigenous knowledge and bush skills among the Western James Bay Cree women of Subarctic Canada. *Hum. Ecol.* **25**, 197–222 (1997).
30. R. Aunger, The life history of culture learning in a face-to-face society. *Ethos* **28**, 445–481 (2000).
31. S. J. Shennan, J. Steele, "Cultural learning in hominids: A behavioral ecological approach" in *Mammalian Social Learning: Comparative and Ecological Perspectives*, H. O. Box, J. R. Gibson, Eds. (Cambridge University Press, 1999), pp. 367–388.
32. B. S. Hewlett, H. N. Fouts, A. H. Boyette, B. L. Hewlett, Social learning among Congo Basin hunter-gatherers. *Philos. Trans. R. Soc. B* **366**, 1168–1178 (2011).
33. B. S. Hewlett, C. J. Roulette, Teaching in hunter–gatherer infancy. *R. Soc. Open Sci.* **3**, 150403 (2016).
34. S. Gallois, R. Duda, B. Hewlett, V. Reyes-García, Children's daily activities and knowledge acquisition: A case study among the Baka from southeastern Cameroon. *J. Ethnobiol. Ethnomed.* **11**, 86 (2015).
35. S. Lew-Levy *et al.*, Who teaches children to forage? Exploring the primacy of child-to-child teaching among Hadza and BaYaka Hunter-Gatherers of Tanzania and Congo. *Evol. Hum. Behav.* **41**, 12–22 (2020).
36. N. Blurton Jones, K. Hawkes, J. F. O'Connell, "Modelling and measuring costs of children in two foraging societies" in *Comparative Socioecology: The Behavioural Ecology of Humans and Other Mammals*, V. Standen, R. Foley, Eds. (Blackwell Scientific, 1989), pp. 367–390.
37. D. W. Bird, R. Bliege Bird, "Martu children's hunting strategies in the Western Desert, Australia" in *Hunter-Gatherer Childhoods: Evolutionary, Developmental, and Cultural Perspectives*, B. S. Hewlett, M. E. Lamb, Eds. (Aldine Transaction, 2005), pp. 129–146.
38. C. M. Turnbull, *The Forest People* (Simon & Schuster, 1962).
39. M. Konner, "Relations among infants and juveniles in comparative perspective" in *Friendship and Peer Relations*, M. Lewis, L. A. Rosenblum, Eds. (John Wiley and Sons, 1976).
40. G. D. Salali *et al.*, Development of social learning and play in BaYaka hunter-gatherers of Congo. *Sci. Rep.* **9**, 11080 (2019).
41. A. H. Boyette, Children's play and culture learning in an egalitarian foraging society. *Child Dev.* **87**, 759–769 (2016).
42. S. Lew-Levy, A. H. Boyette, Evidence for the adaptive learning function of work and work-themed play among Aka forager and Ngandu farmer children from the Congo Basin. *Hum. Nat.* **29**, 157–185 (2018).
43. S. J. Dira, B. S. Hewlett, "Learning to spear hunt among Ethiopian Chabu adolescent hunter-gatherers" in *Social Learning and Innovation in Contemporary Hunter-Gatherers: Evolutionary and Ethnographic Perspectives*, B. S. Hewlett, H. Terashima, Eds. (Springer Japan, 2016), pp. 71–82.
44. J. Lewis, "Play, music and taboo in the reproduction of an egalitarian society" in *Social Learning and Innovation in Contemporary Hunter-Gatherers: Evolutionary and Ethnographic Perspectives*, B. S. Hewlett, H. Terashima, Eds. (Springer Japan, 2016), pp. 147–158.
45. S. Lew-Levy *et al.*, Costly teaching contributes to the acquisition of spear hunting skill among BaYaka forager adolescents. *Proc. R. Soc. B* **289**, 20220164 (2022).
46. P. Jordan, *Technology as Human Social Tradition: Cultural Transmission among Hunter-Gatherers* (University of California Press, 2015).
47. S. Lew-Levy, A. Milks, F. Kiabiya Ntamboudila, T. Broesch, M. A. Kline, BaYaka adolescent boys nominate accessible adult men as preferred spear hunting models. *Curr. Anthropol.* **62**, 631–640 (2021).
48. V. Reyes-García, S. Gallois, K. Demps, "A multistage learning model for cultural transmission: Evidence from three Indigenous societies" in *Social Learning and Innovation in Contemporary Hunter-Gatherers*, H. Terashima, B. S. Hewlett, Eds. (Springer Japan, 2016), pp. 47–60.
49. M. R. Kisliuk, *Seize the Dance!: BaAka Musical Life and the Ethnography of Performance* (Oxford University Press, 1998).
50. A. H. Boyette, data_PNAS_fig1.csv. GitHub. https://github.com/ahboyette/Hewlett_etal_2024_PNAS_SI. Deposited 5 August 2024.
51. L. Cavalli-Sforza, M. W. Feldman, Models for cultural inheritance I. Group mean and within group variation. *Theor. Popul. Biol.* **4**, 42–55 (1973).
52. L. L. Cavalli-Sforza, M. W. Feldman, K. H. Chen, S. M. Dornbusch, Theory and observation in cultural transmission. *Science* **218**, 19–27 (1982).
53. D. Bombjaková, "The role of public speaking, ridicule, and play in cultural transmission among Mbendjele BaYaka forest hunter-gatherers", PhD, Department of Anthropology, University College London, London (2018).
54. R. B. Lee, *The Dobe Ju/'Hoansi* (Wadsworth Cengage Learning, ed. 4, ed. Student, 2013).
55. A. N. Crittenden, "To share or not to share? Social processes of learning to share food among Hadza hunter-gatherer children" in *Social Learning and Innovation in Contemporary Hunter-Gatherers*, H. Terashima, B. S. Hewlett, Eds. (Springer Japan, 2016), pp. 61–70.
56. J. Bowlby, *Attachment* (Basic Books Inc., 1969).
57. B. S. Hewlett, M. E. Lamb, B. Leyendecker, A. Schölmerich, Internal working models, trust and sharing among foragers. *Curr. Anthropol.* **41**, 287–297 (2000).
58. H. S. Kaplan, K. Hill, J. Lancaster, M. Hurtado, A theory of human life history evolution: Diet, intelligence, and longevity. *Evol. Anthropol.* **9**, 156–185 (2000).
59. N. Quinn, Ed., *Advances in Culture Theory from Psychological Anthropology* (Springer International Publishing, 2018).
60. P. Bourdieu, *Outline of a Theory of Practice* (Cambridge University Press, 1977).
61. B. Rogoff, R. Paradise, R. M. Arauz, M. Correa-Chávez, C. Angelillo, Firsthand learning through intent participation. *Annu. Rev. Psychol.* **54**, 175–203 (2003).
62. J. Woodburn, Egalitarian societies. *Man* **17**, 431–451 (1982).
63. B. S. Hewlett, M. E. Lamb, "Integrating evolution, culture and developmental psychology: Explaining caregiver–infant proximity and responsiveness in central Africa and the USA" in *Between Culture and Biology: Perspectives on Ontogenetic Development*, H. Keller, Y. H. Poortinga, A. Schölmerich, Eds. (Cambridge University Press, 2002), pp. 241–269.
64. F. W. Marlowe, Marital residence among foragers. *Curr. Anthropol.* **45**, 277–284 (2004).
65. S. Mathew, C. Perreault, Behavioural variation in 172 small-scale societies indicates that social learning is the main mode of human adaptation. *Proc. R. Soc. B* **282**, 20150061 (2015).
66. M. Tomasello, *The Cultural Origins of Human Cognition* (Harvard University Press, 1999).
67. L. Fogarty, P. Strimling, K. N. Laland, The evolution of teaching. *Evolution* **65**, 2760–2770 (2011).
68. B. L. Hewlett, Social learning and innovation in adolescence: A comparative study of Aka and Chabu hunter-gatherers of central and Eastern Africa. *Hum. Nat.* **32**, 239–278 (2021).
69. J. Smallwood, J. Andrews-Hanna, Not all minds that wander are lost: The importance of a balanced perspective on the mind-wandering state. *Front. Psychol.* **4**, 441 (2013).
70. K. Hawkes, J. O'Connell, N. Blurton Jones, E. L. Charnov, Grandmothering, menopause, and the evolution of human life histories. *Proc. Natl. Acad. Sci. U.S.A.* **95**, 1336–1339 (1998).
71. H. Jang *et al.*, Women's subsistence networks scaffold cultural transmission among BaYaka foragers in the Congo Basin. *Sci. Adv.* **10**, eadj2543 (2024).